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INHERITANCE OF DEMOGRAPHIC AND PRODUCTION PARAMETERS IN THE MARINE COPEPOD *EURYTEMORA HERDMANI*

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The traits referred to in this report—body size, age of maturity, survivorship, and sex ratio—are important in demography and production of copepods. Biometrical techniques of quantitative or variance genetics are used to estimate the variance among individuals attributable to genetic and environmental sources. The book by Falconer (1960) remains an excellent introduction. Of particular interest is the heritability (h^2) of a trait, which is the ratio of the additive genetic variance to the total phenotypic variance in a population in defined circumstances. Estimation of h^2 allows one, in principle, to predict the response of a trait to selection, at least over a few generations. The techniques of quantitative genetics have been developed largely for use in animal and plant breeding for agriculture and commerce. Studies of the ecological genetics of natural populations have traditionally depended on distinguishable polymorphisms. No mention is made of quantitative genetics in a recent review of the mechanisms of evolution and population genetics of marine organisms (Gooch, 1975), although there are a handful of recent studies (*e.g.*, Chapman, 1974; Doyle, 1974).

The few genetic studies of copepods have been directed at Mendelian traits showing variation within populations, or to differences between local populations in certain quantitative traits (*e.g.*, Battaglia, 1970). Copepods are particularly suitable for applications of quantitative genetics to variation within populations. Earlier work shows that sizes, fecundities, and development rates of a number of copepods are predictable functions of temperature when they are adequately fed (Corkett and McLaren, 1969, 1970). Thus, experimental (environmental) variance can be minimized by controlling temperatures and proffering excess food. The results of such experiments can also be readily translated into demographic models of natural populations (McLaren, 1974).

The copepod *Eurytemora herdmani* Thompson and Scott 1897 is a widespread neritic species. In the western North Atlantic it occurs between northern Labrador (Carter, 1965) and Chesapeake Bay (Heron, 1964). Around Halifax it is common throughout the year and is at times the most abundant copepod in the upper few meters.

MATERIALS AND METHODS

The biometrical analyses of quantitative genetics require rearing of individuals or groups of individuals of known parentage in environments that are as uniform as possible or that differ randomly with respect to the individuals or groups. For the present experiments, female stage V copepodites were removed from fresh plankton samples and given excess food until they matured. Adult males were placed, one to a bottle, in a series of 125 ml bottles and several unfertilized females placed with each of them. Fertile egg sacs usually appeared within hours on some of these females. The females were then isolated in bottles at the temperature at which their offspring were to be reared, and their newly hatched nauplii were removed with fine transfer pipets and placed in labelled vials or bottles.

The keeping of copepods in the laboratory has become commonplace, but the rearing of large numbers of separated individuals is highly laborious. These individuals or small groups were kept in vials or bottles in temperature-controlled rooms, randomly disposed under a variable cycle of diffuse light (usually about 15D : 9L). The rearing medium was membrane-filtered, autoclaved, natural sea water, enriched according to the prescription of Lewis (1967). The containers were swirled usually about three times daily. The animals were removed by fine pipets regularly and their medium and food changed. Sometimes they had to be disentangled from detritus with the aid of fine needles. The food organisms were the flagellate *Isochrysis galbana* and the diatom *Thalassiosira* sp., both reared axenically on half-strength "*f*" medium (Guillard and Ryther, 1962). Each of the three experiments analyzed here differed in ways that are detailed below.

The first experiment (hereafter the 15° C experiment) was begun with 14 males and 28 females captured as copepodites in early May, 1974. Each male fertilized two females and their nauplii all hatched 1000–1900 hr on May 11. Forty-four nauplii from each female were placed, four to a vial, in 25 ml vials. Rearing temperatures, monitored twice daily, ranged from 14.6–15° C (mean 14.9 ± 0.02). The young were fed 75 ml each of six-day-old cultures of *Isochrysis* and *Thalassiosira* made up to one liter with rearing medium. This was changed every fifth day. The diatom did not stay in suspension well and was not used in later experiments. *Isochrysis* flourished in the rearing medium, which remained noticeably green at all times. A few haemocytometer counts during the experiment indicated concentrations of about 1 to 3×10^5 cells per ml, probably far in excess of requirements for maximal growth rates (Corkett and McLaren, 1970). The first offspring matured on May 25, and thereafter the vials were examined in random order every eight hours, a procedure that took some hours while most remained immature.

The second experiment (hereafter the 10° C experiment) was begun with 15 males, each mated to 2 females, both sexes having been reared from wild-caught stage V copepodites. Their nauplii hatched 1000–1700 hr on June 17, 1974. Twenty from each female were reared at 10.0 ± 0.03° C in individual 15 ml vials, which were changed to 25 ml when they began to molt into copepodites. They were fed 150 ml of six-day-old *Isochrysis* made up to one liter with rearing medium, changed every fifth day. The offspring began to mature on July 8 and were checked three times daily thereafter.

The third experiment (hereafter the 12.5° C experiment) was designed for analysis of regressions of offspring sizes on parent sizes. The female parents were chosen to obtain extreme size differences from among large numbers reared from stage V copepodites in each August, 1975. The males were chosen as adults from a large sample from nature. Roughly equal numbers of matings of small × small, medium × medium, large × large, and small × large (for both sexes) were attempted. Offspring from successful matings were fed every fourth day with 225 ml of five-day-old *Isochrysis* made up to one liter with rearing medium. At 12.6 ± 0.02° C, they began to mature on August 9 and were examined daily thereafter.

Ages of maturity were determined to the nearest 0.3 day for the 10° C and 15° C experiments. Offspring were measured at 50× with an optical micrometer, estimating to the nearest 2 μ. Cephalothorax lengths were measured along the dorsal mid-line of the cephalothorax.

A widely used experimental design to estimate heritability (h^2) of a trait in offspring involves mating each male parent (sire) to more than one female (dam). The resulting measurements from offspring are treated by one-way, multilevel, hierarchical (nested) ANOVA, from which components of variance can be determined for each level: between sires, between dams within sires, between replicates (where offspring are reared in within-family groups), and within families. Since it is not possible to prevent differences in mortality, corrections must be made for unequal class sizes. The calculations are fully described by Sokal and Rohlf (1969), whose FORTRAN program was used.

Variance components can be summed and the component for each level expressed as a percentage of this total. This percentage is the intraclass correlation coefficient for the level. The intraclass correlation coefficient between sires is of particular interest as it is a measure of the h^2 of the particular trait that is uninfluenced by possible maternal or common-environment effects. The comparison is between families with the same sire but with different dams; that is, between half sibs with one-fourth of their genetic material in common. So the intraclass correlation coefficient is multiplied by four to give the estimated h^2. The same reasoning applied to the variance component between dams within sires gives an estimate of h^2 that includes any maternal effects. If the dam component is not significantly larger than the sire component, the two may be combined to give a more reliable estimate of the h^2, based on additive genetic effects alone.

Falconer (1963) gives formulas for calculation of symmetrical standard errors of h^2. Since intraclass correlation coefficients are based on variances, confidence intervals should be calculated from F-tables and are asymmetrical. Techniques for calculating such intervals from ANOVA with unequal class sizes are given by Haggard (1958), but this leads to awkwardness. Negative variance components and lower 95% confidence limits are readily ascribable to sampling error, and are traditionally expressed as zero. However, upper confidence limits in excess of 1.0 (the theoretical maximum) were found for a number of estimates of h^2 in this study. For these reasons, confidence intervals for h^2 estimated from ANOVA of sib values are not presented. Rather, probabilities that the estimates differ from zero based on the associated F-tests are given, although this *a posteriori* setting of probabilities can be faulted also.

ANOVA of sib values is an inefficient (although sometimes the only) method of estimating h^2. An alternate estimation is from the regression of the mean value of the trait among sibs against its value in parents. Ordinarily h^2 is taken as equal to the regression coefficient (b) of offspring values on their mid-parent values, or as twice the b of offspring on single parents (each contributing half the genetic material to offspring). Since number of offspring within families varies, the mean family values must be weighted according to the procedure of Kempthorne and

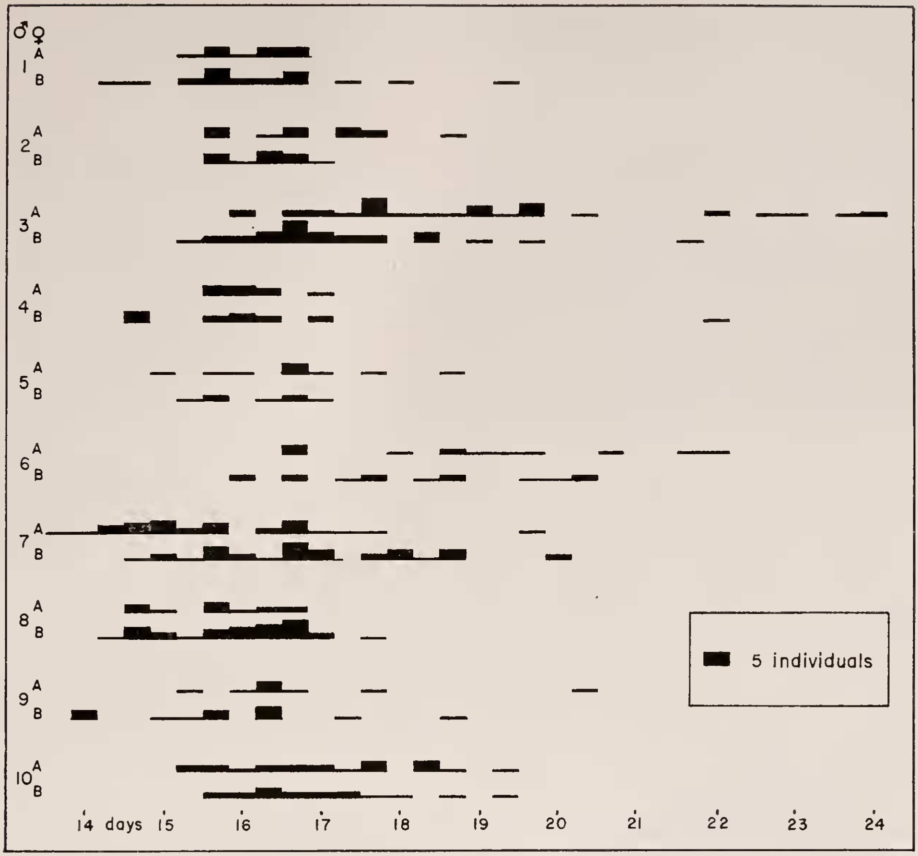

FIGURE 1. Freqeuncy distributions of ages of maturity in female offspring of *E. herdmani* at 15° C. Only families with more than six offspring are included in the figure.

Tandon (1953), as modified by Falconer (1963). This corrects for slope-dependent variance and for the intraclass correlation of families. Falconer's "reasonable estimate" of s.e.$_b$ makes use of the weighted sums of squares and sums of weights as number of degrees of freedom and is used here. Other statistical matters are considered below in context.

RESULTS

Age at maturity

Average times from hatching to maturity were about 28 days at 10° C and about 16 days at 15° C, the females taking longer. These are slightly shorter than the "generation times" (not clearly defined) for this species in the laboratory as given by Katona (1970).

The kinds of data analyzed are shown in Figure 1, on which it is evident that there is a great deal of variation among individuals. Yet, parental effects are

TABLE I

ANOVA and heritability estimates of time to maturity of offspring of E. herdmani.

Temperature	Sex of offspring	Source of variance	Mean square	Per cent of total variance	d.f.	h^2	P
10° C	Male	Between sires	41.60	2.6	14	0.10	0.45
		Between dams, within sires	32.81 (35.03)*	10.4	14 (11.5)	0.42	0.06
		Within families	20.41	87.0	133	—	—
	Female	Between sires	23.28	4.9	14	0.20	0.30
		Between dams, within sires	16.67 (16.60)	0.3	15 (8.7)	(0)	0.50
		Within families	16.88	95.4	85	—	—
15° C	Male	Between sires	12.43	−3.7	13	(0)	0.68
		Between dams, within sires	12.26 (14.72)	28.3	14 (13.2)	1.13	<0.0001
		Between replicates	2.26 (2.26)	16.9	203 (200.9)	—	<0.0001
		Within replicates	1.45	58.5	219	—	—
	Female	Between sires	24.82	17.7	13	0.71	0.05
		Between dams, within sires	8.24 (9.96)	17.7	15 (13.5)	0.72	<0.001
		Between replicates	2.00 (2.02)	8.8	185 (174.9)	—	<0.001
		Within replicates	1.53	55.9	210	—	—

* Terms in parentheses adjusted for unequal class sizes.

also clear; the effects of the male parent are seen, for example, by comparison of the families of male 6 and male 8, and the contribution of females is evident in the two families of male 7.

The 15° C experiment involved up to four surviving animals in each replicate vial, and the component of variance attributable to differences between vials within families is relatively low (Table I). The differences within replicates do, however, include environmental effects to the extent that "accident" plays a role in maturation rate. A distressing feature of these large-scale rearings are a few "stragglers" that matured some time after the others. The delays were not nearly as extreme as those found among species of harpactacoid copepods by Coull and Dudley (1976), who believe that the spread in times within families is adaptive. Probably stragglers of *E. herdmani* had been subjected to some stress or disease during rearing; some were known to have spent time entangled in detritus. There is no obvious way of transforming distributions when only some are skewed this way, although the variances may be inhomogeneous and formally inappropriate for ANOVA. Transformation to ranks might help, but rank ANOVA does not seem to have been fully explored for multilevel cases with unequal class sizes. For present purposes, the effect of "stragglers" is to reduce intraclass correlation coefficients and therefore estimates of h^2.

The ANOVA (Table I) indicates that age of maturity was strongly and significantly heritable only for female offspring in the 15° C experiment. The very similar between-sire and between-dam components suggest that there was no additional maternal contribution in this experiment. In the 10° C experiment female age of maturity was not significantly heritable, nor was there any detectable maternal effect. The results for male offspring are to a degree consistent between the two experiments: age of maturity was not significantly heritable, but there were powerful maternal effects.

Adult size

The ANOVA (Table II) indicates that size was strongly heritable only among males in the 15° C experiment. The between-dam, within-sire components for both male and female offspring were similar to the between-sire components in the 15° C experiment. This suggests that there were no maternal effects and that the between-sire estimate of h^2 in size of female offspring, although not itself significant, is real. In the 10° C experiment there were low, nonsignificant estimates of h^2 and strong maternal effects.

Estimates of h^2 in size were also derived from regressions (*e.g.*, Fig. 2). Some of the parents in the 10° C and 15° C experiments died and disintegrated before they could be measured.

In using mid-parent values or the sib and dam values separately, it has to be assumed that the population variance of the trait are the same in males and females. However, dams of *E. herdmani* were distinctly more variable in length than were sires (F, 2.50; d.f., 25, 14, at 10° C; F, 7.01; d.f., 12, 7, at 15° C). The same was true for offspring (F, 2.14; d.f., 103, 140, at 10° C; F, 1.29; d.f., 181, 222, at 15° C). In view of these disparities, it was necessary to equalize standard deviations (using average s.d. of the two sexes) for parents and offspring, respectively, within each experiment. This ensured that each parent contributed comparably to the

TABLE II

ANOVA and heritability estimates of adult size of offspring of E. herdmani.

Temperature	Sex of offspring	Source of variance	Mean square	Per cent of total variance	d.f.	h^2	*P*
10° C	Male	Between sires	7.54	−0.7	14	(0)	0.52
		Between dams, within sires	7.11 (7.87)*	18.7	14 (11.9)	0.75	0.01
		Within families	3.32	82.0	132	—	—
	Female	Between sires	13.12	6.0	14	0.24	0.35
		Between dams, within sires	8.96 (10.36)	23.3	15 (11.9)	0.93	0.02
		Within families	4.29	70.0	85	—	—
15° C	Male	Between sires	33.59	24.2	13	0.97	0.04
		Between dams, within sires	9.69 (11.60)	18.9	14 (13.1)	0.76	0.001
		Between replicates	2.04 (2.05)	15.5	202 (199.6)	—	0.007
		Within replicates	11.84	41.3	215	—	—
	Female	Between sires	22.41	9.6	13	0.38	0.14
		Between dams, within sires	10.42 (11.60)	12.0	13 (11.9)	0.48	<0.001
		Between replicates	3.67 (3.68)	15.4	188 (185.9)	—	<0.001
		Within replicates	2.49	63.0	205	—	—

* Terms in parentheses adjusted for unequal class sizes.

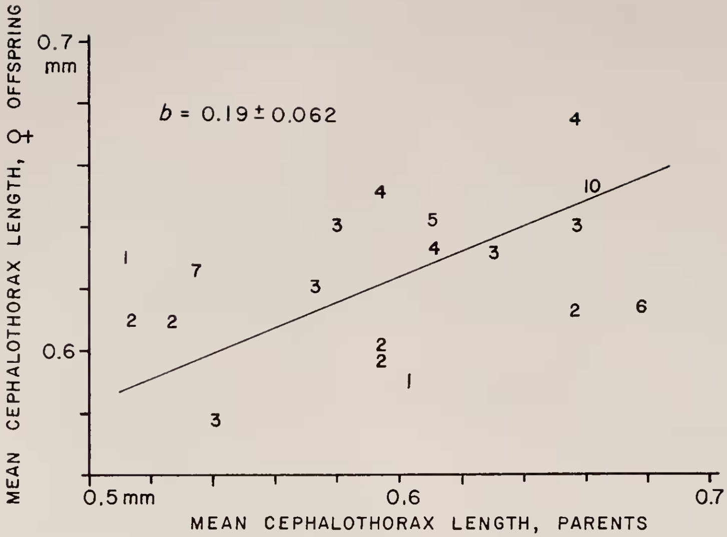

FIGURE 2. The relationship between mean parent size and mean size of female offspring at 12.5° C. The numbers are family sizes used in calculating weights for means used in the regression.

mid-parent value and that *b* for different parent-offspring regressions was not sex-dependent.

The results of regression analysis (Table III) reinforce conclusions from ANOVA (*cf.*, Table II). Heritabilities were high at 15° C and low, although still significant from midparent regressions, at 10° C. The indication of maternal effects in ANOVA may be reflected in the high values of h^2 from regressions on dams; it is

TABLE III

Estimates of heritabilities of adult size of offspring of E. herdmani *based on parent-offspring regressions*

Temperature	Regression	d.f.*	b	h^2	s.e. h^2
10° C	Male offspring vs. mean parent	87.1	0.180	0.18	0.104
	Male offspring vs. male parent	86.1	−0.180	−0.36†	0.181
	Male offspring vs. female parent	92.4	0.233	0.47	0.151
	Female offspring vs. mean parent	64.3	0.166	0.17	0.061
	Female offspring vs. male parent	75.2	−0.316	−0.63†	0.209
	Female offspring vs. female parent	84.7	0.444	0.89	0.161
12.5° C	Male offspring vs. mean parent	52.7	0.185	0.19	0.046
	Female offspring vs. mean parent	39.5	0.191	0.19	0.062
15° C	Male offspring vs. mean parent	33.8	0.608	0.61	0.118
	Male offspring vs. male parent	48.3	0.368	0.74	0.107
	Male offspring vs. female parent	22.0	0.194	0.39	0.378
	Female offspring vs. mean parent	65.8	0.514	0.51	0.153
	Female offspring vs. male parent	68.1	0.300	0.60	0.149
	Female offspring vs. female parent	45.9	0.203	0.41	0.399

* Sum of weights of the means used in the regressions (see text).

† Negative values of h^2 are not theoretically possible.

as though the effect were mediated through female size. The accompanying negative values for sires are inexplicable.

Since some parents for the 12.5° C experiment were chosen for extreme sizes, population variances cannot properly be estimated. Furthermore, their male and female offspring turned out to be similar in length variation (F, 1.06; d.f. 65, 102). Therefore no attempt was made to equalize standard deviations for estimates of b and h^2. The mid-parent values of h^2 for size at 12.5° C are low, but with substantially reduced s.e. compared with those at 10° C. Of course single-parent estimates of b in the 12.5° C experiment would be artificially biased upward by correlation of parent sizes and were not used to calculate h^2.

Parental selection or assortative mating itself should cause only negligible bias in regression estimates as long as h^2 is low (Hill, 1970). However, there could have been another source of bias in the 12.5° C experiment. The dams were matured from stage V copepodites, which were probably a near-cohort that had experienced a common environment. The sires, however, were taken as adults in nature in order to maximize the available size range. They may have matured over a period of time in a variety of conditions. Increased environmental variance in their sizes would have the effect of depressing estimates of b for offspring on sires as compared with dams. However, there is no evidence that this happened. Estimates of $b \pm \text{s.e.}_b$ for offspring on single parents were: 0.11 ± 0.042 for males on males; 0.20 ± 0.045 for males on females; 0.16 ± 0.051 for females on males; and 0.15 ± 0.063 for females on females. (The implied, but invalid, estimates of h^2 are larger than those from mid-parent regressions for reasons noted above.) It is concluded that, in spite of differences in experimental design, the results at 12.5° C are comparable with those from the other two experiments.

Correlation of size and age of maturity

Increase in temperature decreases development time and normally decreases size of copepods (Deevey, 1960; McLaren, 1974). However, as Katona (1970) had already shown, temperature may not influence size of *E. herdmanii*; means and s.e. were 671 ± 7 μ and 667 ± 5 μ for males and 769 ± 6 μ and 758 ± 15 μ for females at 10° C and 15° C, respectively. Furthermore, size and age of maturity were not inversely related within experiments. This is adequately demonstrated without analysis of covariance with two simple nonparametric tests.

The rank correlations between family medians of sizes and ages of maturity (Table IV) were all negative and highly significant except for female offspring at 15° C. Within families, the individuals born before the median age of maturity

Table IV

Spearman rank correlation of median cephalothorax lengths and median times to maturity among families of E. herdmani.

Temperature	Sex	r_s	d.f.	P
10° C	Male	−0.61	24	0.01
	Female	−0.66	20	0.01
15° C	Male	−0.53	23	0.01
	Female	−0.15	23	0.48

Table V

ANOVA for binomial data of mortality of E. herdmani *before maturity. Estimates of* h^2 *made after probit transformation (see text).*

Temperature	Source of variance	Mean square	Per cent of total variance	d.f.	h^2	s.e. h^2
10° C	Between sires	0.384	0.3	14	0.01	0.107
	Between dams, within sires	0.352	2.3	15	0.08	0.111
	Within families	0.244	97.5	570	—	—
15° C	Between sires	0.643	0.4	13	0.02	0.043
	Between dams, within sires	0.575	4.2	14	0.13	0.101
	Within families	0.196	95.4	1204	—	—

were more likely to be larger than median size. At 15° C the numbers were 103:57 for males and 86:57 for females. At 10° C the numbers were 53:14 and 31:6, respectively. Again only for females at 15° C is this not significant (by Chi^2, corrected for continuity).

It thus appears that small adults on average took longer to mature. This implies that heritabilities of growth rates (size/time) would be higher than those for sizes and ages of maturity separately.

Mortality

Mortality was 52% at 10° C and 29% at 15° C; but since maturation time averaged longer at 10° C, instantaneous death rates were quite similar: 0.025 at 10° C and 0.021 at 15° C on a daily basis. Mortality was quite variable between families, and it is of some interest to calculate heritabilities. Mortality is not a continuous trait in individuals, but can be thought of as a threshold phenomenon expressed when the sum of independent, normally distributed environmental and genetic components exceeds a certain "dose." Intraclass correlation coefficients can be estimated from ANOVA for binomial data (Lush, Lamoreux and Hazel, 1948). The additive heritabilities on the observed probability scale can then be calculated after probit transformation (Dempster and Lerner, 1950 and references therein).

Although the ANOVA (Table V) indicates a highly significant between-dam, within-sire component at 15° C (F, 2.94; d.f. 14, 1204), the heritability estimates are small and do not differ from zero, according to their standard errors. These symmetrical s.e., calculated as suggested by Dempster and Lerner (1950), are only approximate. The above F-test and the fact that the between-dam estimates of h^2 are substantially higher than the between-sire ones at both 10°C and 15° C suggest that there is a real maternal effect on survivorship.

Sex ratio

Overall sex ratios (male/total) were 162/281 (58%) at 10° C and 450/827 (51%) at 15° C. These ratios do not differ significantly from one another (Chi^2, corrected for continuity, 3.18; P, 0.07).

Individual families varied markedly, some being all males and others all females. Six ratio can be treated as a threshold trait using the analyses applied above to mortality. In this case, the unequal class sizes called for use of adjusted d.f. in calculating F ratios and s.e. (Table VI). Both sire and dam appeared to influence sex ratios of their families equally at both temperatures, so that intraclass correlation coefficients can be combined to give more reliable estimates for h^2 of sex ratio of 0.12 ± 0.13 (adjusted d.f. 18.7) at 10° C and 0.30 ± 0.13 (adjusted d.f. 62.8) at 15° C. A significant effect at 15° C is also implied in the F-ratios (from mean squares on Table VI).

Sex ratios were distinctly bimodal among the families at 15° C and probably at 10° C as well (Fig. 3). This suggests that there is major-gene control of high-male and low-male status of families, with polygenic overlay of variance. Since low-male families occurred in both families of two sires and in only one family of three other sires, the major-gene control appears to be autosomal.

For convenience, within-vial variance was ignored in the ANOVA of sex ratio at 15° C, and this might have inflated the estimated h^2 to the extent that it is environmentally influenced. Although Katona (1970) found no correlation between sex ratio and number of progeny in a tube (no data given) for *Eurytemora* (sp.?), the possibility of more subtle effects was worth checking. These could result, for example, from pheromonic influences so that extreme sex ratios (maximally 0/4 or 4/4) were promoted. Among vials with 4 survivors in 13 families with reasonably balanced ratios (39–72% male), the expected frequencies of extremes (0/4, 4/4) were calculated from binomial expectations, using family ratios as p:q. The observed number of extremes (9) was very close to the expected (10.9).

Given the distorted sex ratios, it is possible that some individuals of one sex tended to have attributes of the other. For example, females average larger in size and slower in maturation than males, and heritable sex ratios could have influenced the h^2 of size and age of maturity within sexes. However, female offspring in low-male families do not differ significantly (randomized test, Siegel, 1956) from those in high-male families in median body size (t, 1.22; d.f., 25) or median age of maturity (t, 1.08; d.f., 25). The medians for male offspring in low-male families are based at most on a few individuals, but also appear to fall within the range for high-male families. It is concluded that offspring are "real" males and females for our purposes.

TABLE VI

ANOVA for binomial data of sex ratio in offspring of E. herdmani. *Estimates of* h^2 *made after probit transformation (see text).*

Temperature	Source of variance	Mean square	Per cent of total variance	d.f.	h^2	s.e. h^2
10° C	Between sires	0.479	3.4	14	0.11	0.218
	Between dams, within sires	0.317	3.9	15	0.13	0.221
	Within families	0.288	92.7	251	—	—
15° C	Between sires	3.454	12.0	13	0.27	0.153
	Between dams, within sires	1.507	16.9	14	0.33	0.171
	Within families	0.180	71.1	849	—	—

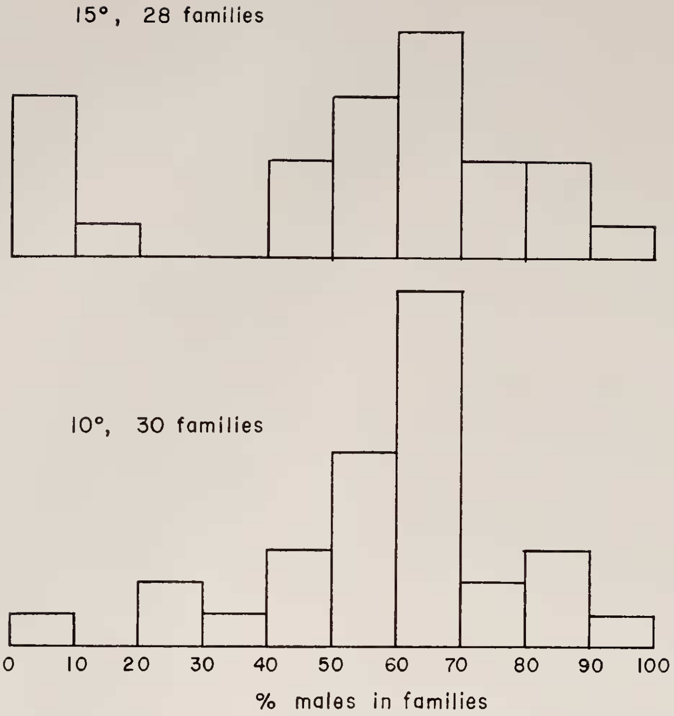

FIGURE 3. Frequency distributions of sex ratios in families of *E. herdmani.*

DISCUSSION

Biological oceanographers have traditional concerns with the effects of salinities, temperatures, and food supplies on marine copepods. In the laboratory, individual variability, if not ignored, is taken as "experimental error." Paffenhöfer (1970) found that differences in size and sex ratios in *Calanus helgolandicus* were correlated with food quantity and quality; but these differences were accompanied by marked variations in mortality, which could have been selective. Furthermore, it is probable that a small number of parents were used to produce the young reared in some of Paffenhöfer's experiments. Certainly the percentage differences between means in some of his experiments are well within the ranges shown by individuals and sometimes family means in the present studies of *Eurytemora herdmani.* This is not a serious criticism of his conclusions, but rather a more general request that precautions be taken (and reported) that minimize effects of inherent differences among experimental copepods.

It is not surprising that genetic differences in quantitative traits are being found between populations of the "same" copepod from different localities (*e.g.*, Carillo, Miller and Weibe, 1974) or even from different seasons (Bradley, 1975). There is a general lack of knowledge concerning the extent of heritable variation *within* populations of copepods and the ecological meaning of this variation in nature. Since this study of *E. herdmani* seems to be the only one of its sort for a planktonic copepod, it is not yet possible to seek clues from comparative studies of the group. However, the result can be compared with more general principles.

Much of the current controversy about genetic variation in nature (Lewontin, 1973) refers to biochemical differences that have no clear effects on the fitness of individuals. It is generally supposed that traits of significance to fitness will have their heritable variation trimmed away by natural selection in the normal environment. Age of maturity and size (which affects female fecundity) are demographic parameters and are clearly components of fitness. Therefore, their generally low heritabilities at 10° C and 12.5° C are not surprising. These temperatures are normal during summer in near-surface waters around Halifax. The much larger heritabilities of size in both sexes and of age of maturity in females in the 15° C experiment are reasonable, since such temperatures rarely occur, even at the surface. Even at this high temperature there are revealing differences between the sexes: heritability of size was lower for females, and age of maturity was not detectably heritable in males. Size is important in determining the egg number of a whole series of clutches in females (Corkett and McLaren, 1969; McLaren, 1974), whereas age of maturity is obviously more important to males, which may fertilize a series of females in short order, but which do not benefit in any obvious way from differences in size.

Although maternal effects are not properly the concern of ecological genetics, they are by no means devoid of interest as adaptive tactics in their own right. In the present experiments there were powerful maternal influences on age of maturity of males, but not females. Conversely, the between-dam component of size was higher for female offspring which, for reasons noted above, would benefit most from this. It is easy to see how the dam could hasten the maturity of her offspring through investments in the egg. Some families of nauplii appeared to have more pigment (lipid?) and to be more vigorous in swimming upon hatching. The stronger between-dam component in morality may also be based largely on differences in early mortality. It is, however, less easy to see how differences in size of adult males could be mediated through a tiny egg.

Unbalanced sex ratios are well known in nature, but difficult to account for in theory (Fisher, 1930; and others since). The discussion by Katona (1970) of the phenomenon in *Eurytemora* in terms of population advantages is naive. Furthermore, the supposed effects shown by him of salinity and temperature will have to be reconsidered in the light of the marked variation among families shown here. The high-male and low-male status of families of *E. herdmani* resembles the occurrence of "sex-ratio," a sex-linked major gene, in *Drosophila* (Policansky, 1974), for which explanations are complicated at best. A careful analysis of genotype-environment interactions in determining sex ratio in *E. herdmani* would probably be revealing.

Finally, although this is the first such study of a copepod, *E. herdmani* should not be taken as "typical." The species around Halifax seems to reproduce more-or-less continuously, with adult males and ovigerous females almost always present, and shows little size variation within samples and through the season. By contrast, the genus *Pseudocalanus* seems to carry eggs sporadically and shows much more size variation in nature. Ongoing studies in this laboratory indicate that there are probably sibling species involved, and that size and age of maturity are much more strongly heritable within populations at natural temperatures.

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SUMMARY

Heritabilities (h^2, the ratio of additive genetic variance to total phenotypic variance) were estimated for a number of traits of *Eurytemora herdmani* from families of known parents reared with excess food at 10°, 12.5°, and 15° C. Age of maturity was strongly heritable only among female offspring at 15° C and size only among male offspring at 15° C. This temperature is extreme for waters near Halifax, Nova Scotia. Low and sometimes nonsignificant heritabilities at 10° and 12.5° C are as expected at these natural temperatures for fitness traits that have had their genetic variance trimmed by natural selection. There were strong maternal (nongenetic) effects on age of maturity of males (which benefit from accelerated maturation) and on size, especially of females (which would benefit from enhanced fecundity). Adult size and age of maturity are negatively correlated, so that growth rate should be even more strongly heritable. There is a suggestion that survivorship (not significantly heritable) is maternally influenced (probably along with development rate) early in life. Unbalanced sex ratios appear to be controlled by a major gene, with polygenic overlay of variance. The genetic variations reported here may be important in the design of experiments with copepods, indicate capacity for quite rapid change of some traits in nature, but should not at this stage be taken as "typical" of marine copepods.

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